STUDIES ON MARINE BRYOZOA. XII. *PORELLA*

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The purpose of the present study is (a) to report two species of *Porella* (Family Smittinidae, Order Cheilostomata, Phylum Bryozoa) from new Antarctic localities, (b) to bring their synonymy up to date, and (c) to add new morphological data to define more clearly their key characters.

The species are from the same bryozoan collection made by the U. S. Navy's 1947–48 Antarctic Expedition as were those of previous studies of this series. Most grateful acknowledgment is due to the National Science Foundation for its very generous and long continued support of this and of previous studies.

Several members of the Family Smittinidae have already been reported (Rogick, 1955, 1956) but the affinities of the two present species were not recognized at that time because one of them had for a long time been known as *Lepralia marginata* while the other so resembled the genus *Cellepora* in general appearance and growth habit that they were put aside for study with the Lepralioid and Celleporid genera. It was only after detailed study that their Smittinid characters became apparent.

GENUS *PORELLA* GRAY 1848

Diagnosis.—Based on Osburn's 1952 and Harmer's 1957 accounts. Frontal a pleurocyst, usually thick and nonperforate except for areolar pores (see fig. 2 A). Suboral avicularium (fig. 2 B) rounded, median, directed proximally, its chamber (fig. 15 C) narrowly connected to a lateral areola on each side. Lyrula absent (fig. 1 R) or slightly developed (fig. 18 M). Ovicell (fig. 2 S) globose, hyperstomial, imperforate, later immersed by secondary calcification (fig. 1 S).

Genotype: *Millepora compressa* Sowerby 1805, selected by Norman 1903, p. 112.

Porella marginata (*Calvet*) *1909*
(*Figures 1–7, 14, 15*)

Synonymy and previous records:

1909. *Lepralia marginata.* Calvet, pp. 24–25; Pl. 2, fig. 7–9. Species was described from a single colony. Ovicell, zooecia, operculum and mandible illustrated. From Bay of Biscoe, 110 meters, on calcareous tube of Annelid.

1924. *Lepralia marginata.* Thornely, p. 11. Found uni- and bilaminate colonies and zooecia with small process on back wall for attachment. From Commonwealth Bay, Sta. 12, 110 fathoms.

1928. *Lepralia marginata.* Livingstone, pp. 6, 8, 9, 10, 60; Pl. 7, fig. 4, 6. Photographs of general appearance of ovicelled and nonovicelled parts of colony. Account mentions strikingly large hinge teeth but does not picture them. Commonwealth Bay (Adelie Land and other stations), 55–157 fathoms.

1952. *Lepralia marginata.* Vigeland, p. 9. Distribution only. From Graham Land, Port Lockroy, 120 meters, on stones and algae.

1957. *Lepralia marginata.* Rogick, p. 8, incidentally mentioned as occurring along with *Phylactellipora lyrulata* at Marguerite Bay, Antarctica Sta. 225.

The above are the only records of this species to date.

Diagnosis.—Zooecial front subhexagonal, finely verrucose (fig. 3, 5), bordered by rounded, closely placed areolae except distally. Orifice (fig. 3 R) straight proximally, arched distally, provided with prominent lateral condyles (fig. 15 F). Avicularium suboral, subcircular, median, placed a slight distance below lower lip (fig. 15 B) and proximally oriented. Avicularial mandible (fig. 6) subsemicircular. Ovicell salient, globose, verrucose, with uncalcified

median pore or pit (fig. 3 T), but becomes completely immersed by secondary calcification. Mural rims (O of fig. 1) of neighboring zoids meet across its front in seams. Hooked processes (fig. 14) on dorsal (basal) surface sometimes.

Morphology.—Considering that only a colony fragment was available to him Calvet illustrated the species admirably. The condyles (fig. 15 F) inside the orifice were not noticed either by Calvet or Thornely but Livingstone reported their presence although he did not figure them. The present account adds further information on this species as measurements, variations in colony appearance in advanced secondary calcification, tentacle sheath and polypide.

Measurements.—The first figures are the minimum, the next the maximum, the last (in parentheses) are the average of ten readings. Measurements are in millimeters. Abbreviations:—L, length; W, width.

0.936–1.368 (1.218) L Zooecia
0.317–0.518 (0.452) W Zooecia
0.145–0.160 (0.159) L Operculum
0.162–0.181 (0.171) W Operculum
0.374–0.418 (0.392) L Ovicell
0.360–0.461 (0.408) W Ovicell
0.087–0.145 (0.111) L Avicularium
0.072–0.101 (0.085) W Avicularium
0.058–0.109 (0.089) L Mandible
0.058–0.087 (0.079) W Mandible

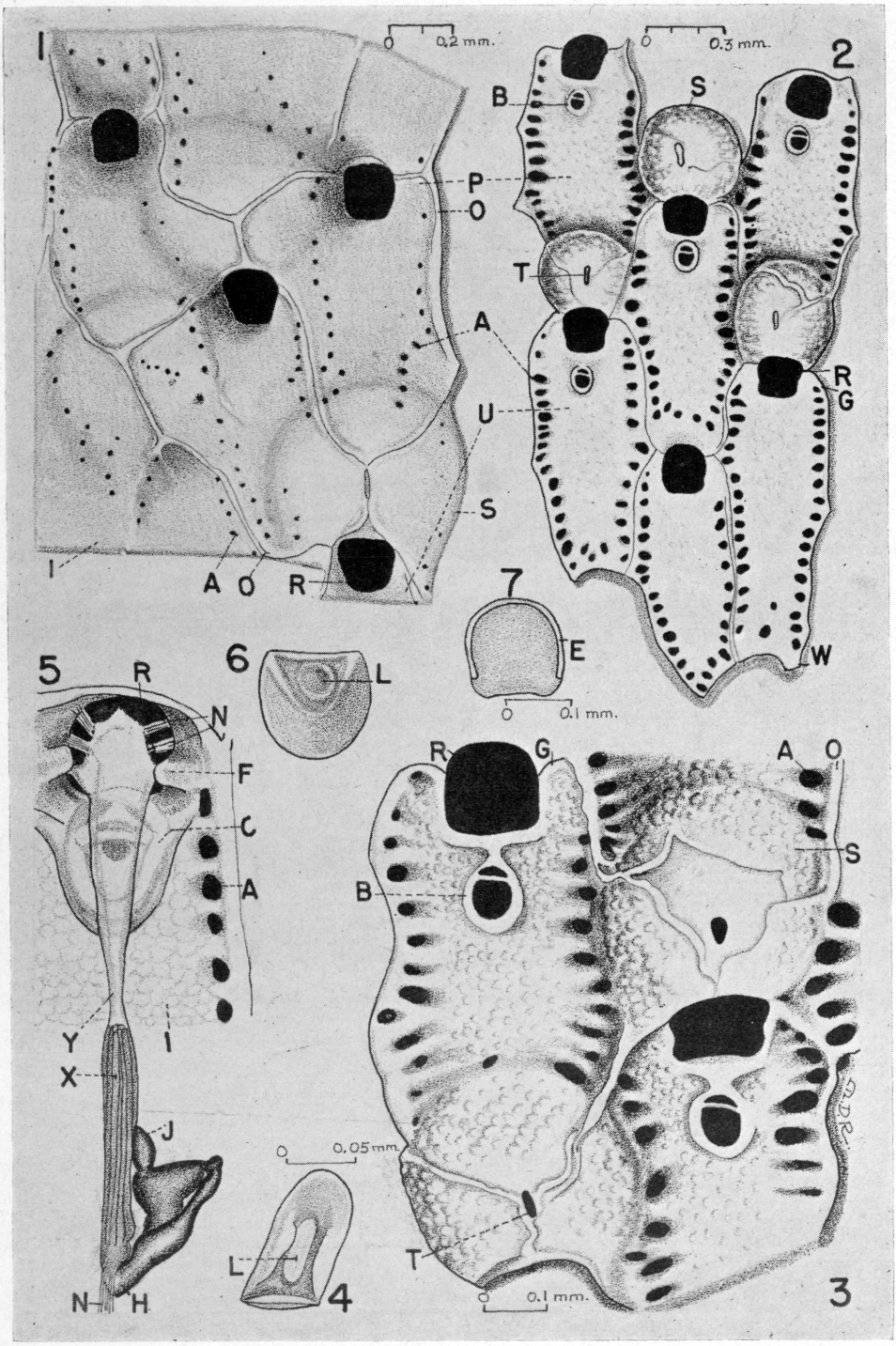
KEY TO ABBREVIATIONS ON FIGURES

A—Areolae
B—Avicularium
C—Avicularial chamber
D—Basal wall of zooecium
E—Chitinous rim of operculum
F—Condyle or articulating ledge
G—Distal end of zoid or zooecium
H—Esophagus of polypide
I—Frontal wall of zooecium
J—Rectum of polypide
K—Lateral wall of zooecium
L—Lucida
M—Lyrula or median tooth
N—Muscles
O—Mural rim or salient line outlining zooecial boundaries
P—Nonovicelled zooecium
Q—Oral spine or spines around orifice
R—Orifice
S—Ovicell
T—Ovicell "pore" or pit
U—Ovicelled zooecium
V—Peristomial wing
W—Proximal end of zooecium
X—Tentacles
Y—Tentacular sheath
Z—Umbo

EXPLANATION OF FIGURES IN PLATE I

All figures on this plate are of *Porella marginata* (Calvet) and were drawn with the aid of a camera lucida.

1. Frontal surface of two nonovicelled and three ovicelled zooecia in an old part of a colony. The orifice of the lower left ovicelled zooecium is completely overgrown. The salient mural rims of the frontal walls of the three neighboring zooecia meet over each ovicell in a Y-shaped seam. Areolar pores which mark the true lateral boundaries of zooecia are fast becoming obliterated. Avicularia are either overgrown or wanting in this part of the colony. Drawn to the scale above.
2. Frontal surface of three ovicelled and three nonovicelled zooecia of a younger colony. Ovivells are not yet overgrown. Drawn to the scale above.
3. Detail of two ovicells and two zooecia. Upper right ovicell shows approximating frontal covering. Drawn to the scale below it.
4. Avicularial chitinous mandible with elliptical lucida and two lateral thickenings. Drawn to the scale directly above it.
5. Inner surface of frontal wall. Polypide is suspended by muscles and tentacular sheath from the operculum region. Operculum is blackened in drawing. Beneath the operculum and behind the long transparent tentacular sheath is visible the avicularial chamber. Drawn to the figure 3 scale.
6. Another avicularial mandible, drawn to figure 4 scale.
7. Operculum, drawn to the scale immediately below it.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Zoarium.—The biggest colony (zoarium), 40 mm long and 21 mm at widest diameter, was hourglass shaped as if it had grown around something. The remaining colony fragments were unilaminar ivory-colored chips measuring from 18 mm by 32 mm downward. Colony surface is quite smooth, neatly patterned. In old colonies smooth areas appear here and there where orifices and frontal pores have been obliterated or covered over by secondary calcification (fig. 1, lower left zoid).

Zooecia.—Zooecia are longer than wide, clearly marked off frontally from each other by a salient rim in young zoids (fig. 2, 3) but not in heavily calcified old zoids. Old zooecial fronts fuse into a common flat crust which is punctured here and there by zooecial orifices and rows of reduced areolar pores (fig. 1). The front of young zooecia is thin, faintly convex, with pebbled (reticulate or verrucose) markings (fig. 5, 15), nonporous except for the closely set areolae which are separated by short ribs. The areolae of old heavily calcified zooecia elongate into tubes of reduced diameter and the ribs lose their identity (fig. 1).

A zoid's frontal wall does not distally encircle its own orifice but stops at the sides of the orifice (fig. 3, upper left zoid).

The lateral zooecial wall has about eight widely spaced pores.

The back (dorsal) wall is slightly convex and provided with one or more median hooked attachment processes (fig. 14) that may wear down or break off into pores.

Orifice.—The orifice is placed at the distal extremity of the frontal wall. It is bounded proximally and laterally by its own frontal wall, distally and laterally by the frontal wall of the next distal zoid.

EXPLANATION OF FIGURES IN PLATE II

All figures were drawn with the aid of a camera lucida.

8. Young 7-spined zooecium of *P. marsupium* from Sta. 226. Avicularium a bit large as compared with other zoids. Avicularial umbo not yet sufficiently developed. Drawn to the scale above it.

9. Frontal view of three zooecia with unfinished developing ovicells and one non-ovicelled zooecium of *P. marsupium* from Sta. 226. Umbones are of variable size. Drawn to the figure 8 scale.

10. View of front and lateral walls of two young *P. marsupium* zooecia, the upper one ovicelled the lower one not. Some spines of the lower one are broken off at the base. The spoutlike aviculiferous umbo, though prominent, is not yet as fully developed laterally as that of figure 12. Lateral wall pores have been omitted from the drawing because they were obscured by adjacent zooecia, so the lateral walls were left in a diagrammatic condition. From Sta. 104. Drawn to the figure 8 scale.

11. Orifice region detail of young *P. marsupium* zoid from Sta. 226. Zoid is slightly older than that of figure 8, with a better developed aviculiferous umbo but with a proportionately smaller avicularium. Drawn to the scale directly below it. Lyrula and condyles faintly visible.

12. Side view of frontal wall of an old ovicelled *P. marsupium* zooecium and the ovicell and peristome of another. The umbo has developed lateral peristomial flaps approximating the ovicell. From Sta. 190.

13. An old ovicelled zoid of *P. marsupium* with roughened "beaded" frontal wall. Spine remnants at sides of ovicell. Peristome not as well developed as in preceding figure. From Sta. 190. Drawn to the figure 8 scale.

14. The basal, back or dorsal walls of four *P. marginata*. Two pointed attachment processes are intact, four have been broken off, leaving holes. From Sta. 226. Drawn to the scale directly above.

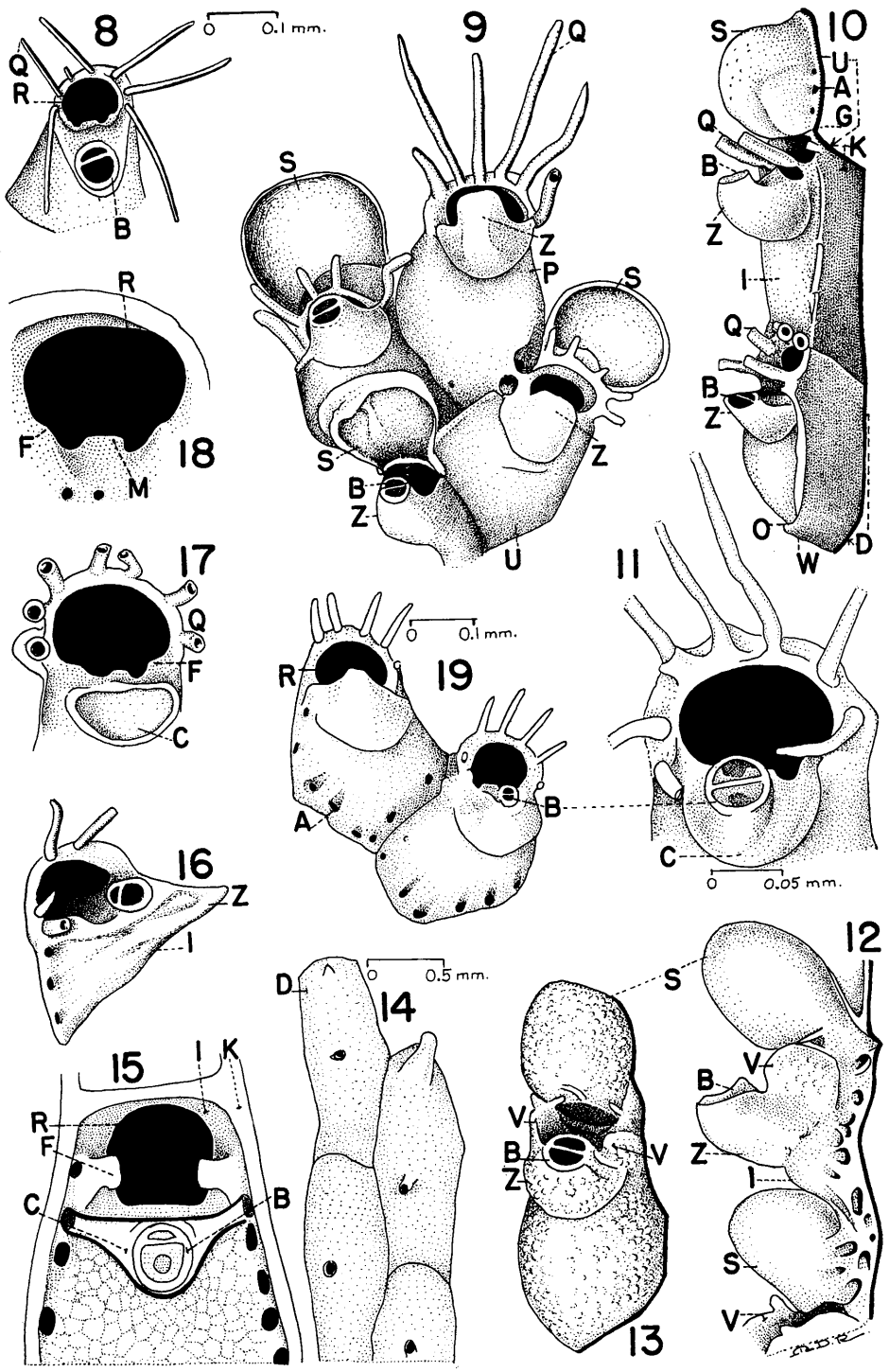
15. Inner surface of frontal wall of *P. marginata* showing orifice, condyles and the bilateral nature of the avicularial chamber. The cobbled pattern of the frontal wall is peculiarly characteristic of young zoids of this species. Drawn to the figure 19 scale.

16. *Porella marsupium* zoid with an incomplete number of spines and an unusually peaked umbo. From Sta. 240 (pebble z). Drawn to the figure 8 scale.

17. Frontal view of orifice and incomplete avicularial chamber of young *P. marsupium* from Sta. 104. The median tooth or lyrula and the lateral condyles or cardelles are evident but the umbo and avicularium have not yet developed. Drawn to the figure 11 scale.

18. Inner surface of frontal wall of *P. marsupium* from Sta. 190, showing shape of orifice and also two small pores which connect to the avicularial chamber in some zoids at least. Drawn to the figure 11 scale.

19. Two young *P. marsupium* zoids from a Sta. 240 colony. Areolae not yet obliterated by crowding or overgrowth. Spine number variable. Drawn to the scale directly above.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The orifice is of the lepralioid type. The primary orifice has a hemispherical anter (distal border or portion) and a poster (proximal region) which is shorter and straighter. The lateral sides of the anter are nearly parallel. The secondary orifice (in older zoids) may be almost round or faintly squared.

Inside the orifice, generally invisible externally, are two strong rectangular or chisel-like condyles, one projecting from each lateral wall.

The operculum is shaped like the primary orifice and provided with a re-inforcing thickened chitinous rim (fig. 7) about its three sides. The operculum fits the orifice externally and articulates internally with the condyles.

Oral spines were absent. Previous workers did not find any either.

Avicularia.—One avicularium per zoid is the usual condition but occasional zoids lack an avicularium (fig. 2). It may be obliterated by secondary calcification (fig. 1). Avicularial size varies slightly but not the shape or location. Avicularia are broadly oval, their rounded beaks directed proximally. They are in the midline a short distance below the orifice, immersed in the frontal wall and parallel to the plane of the basal wall.

The avicularial chamber narrows laterally into a channel which ends at an areola on each side (fig. 15 C). The chamber contains short thick avicularial muscle bundles between which is located the vestigial avicularial polypide.

Ovicells.—The globose, hyperstomial ovicell is not closed by the operculum. In young zoids the ovicell surface is handsomely pebbled and decorated by a thin Y-shaped salient line which is formed by the mural rims of the walls of the three neighboring zoids (lateral and distal) meeting over the ovicell front. At their meeting point a membrane-covered oval pore is usually present. In old heavily calcified zoids the pore may become solidly calcified and obliterated (fig. 1) and the ovicell will no longer protrude but will be immersed in the flat common crust that erases zooecial boundaries and levels zooecial surfaces.

Orange-colored embryos were present in ovicells from Sta. 11.

Polypide.—Polypides are present in some zooecia. The tentacular sheath (fig. 5 Y) is very long, slender, thin, transparent. Two oral glands are located high up near the operculum. It was impossible to get an accurate tentacle count on older zoids but one young bud had 16 tentacles. Tentacles are long and slender (fig. 5 X).

Distribution and ecology.—Porella marginata occurred in small amounts at the following USN Antarctic stations (see Rogick 1956, pp. 222–223 for fuller station details):—Sta. 11 (Lat. 66° 38′ S., Long. 90° E., 150 fathoms); Marguerite Bay Stations 225, 226, 230, 234 (40 fathoms) and Case 1.

A small colony grew on the back of a live *Smittoidea evelinae* (i.e., alive at the time of collection) but other colony fragments were free from any other growths. *Porella marginata* was an unusually "clean" species.

Porella marsupium (*MacGillivray*) *1869*
(*Figures 8–13, 16–19*)

Synonymy and some previous records:

1869. *Lepralia marsupium.* MacGillivray, p. 136. A short description but no figure. From Victoria, Australia.

1879. *Lepralia marsupium.* MacGillivray, pp. 22–23; Pl. 35, fig. 4–4b. Short description. Figures very small with distinctive characters of the 1869 species inadequately illustrated.

1888. *Aimulosia australis.* Jullien, pp. I.59–I.60; Pl. 1, fig. 5 (ovicells and zooecia). Tierra del Fuego, Hoste Isle, Orange Bay.

1895. *Porella marsupium.* MacGillivray, pp. 91–92; Pl. 12, fig. 9a but not Fig. 9 whose lyrula seems too wide.

1904. *Smittia marsupium* (part). Waters, pp. 61–62; Pl. 4, fig. 4. Lat. 70° 23′ S., Long. 82° 47′ W., 480 meters; Lat. 70° S., Long. 80° 48′ W., 500? meters.

1924. *Smittia marsupium?* Thornely, p. 14, mentions 4 or 5 spines. Commonwealth Bay, Adelie Land, 25 fathoms.

1928. *Smittina marsupium?* Livingstone, pp. 7, 65.

1952. *Porella marsupium* (part). Brown, pp. 312–314, fig. 234. Castlecliff, New Zealand. Upper Pliocene.

The following citations are not of the same species:

1881. *Porella marsupium*. Hincks, p. 123; Pl. 1, fig. 6.

1884. *Lepralia marsupium*. Busk, p. 147; fig. 44.

1957. *Smittina marsupium*. Harmer, pp. 922–923; Pl. 63, figs. 11–14.

Discussion.—Calvet (1909, pp. 30–31), Thornely (1924, p. 14), and Livingstone (1928, p. 65) reported the species from Antarctic localities but gave little or no descriptive data and no pictures or measurements of it and for these reasons their records were not included in the foregoing synonymy since this early became a controversial species. Hincks (1881), Busk (1884), and Harmer (1957) on the other hand illustrated their *marsupium* but appear to have had another species than that of MacGillivray.

The USN specimens agreed well in measurements with Brown's Castlecliff Pliocene forms, except that the orifice length (height) measurements of the USN zoids were a bit greater. Also, Brown's species had four oral spines while the USN zoids had five to seven.

Diagnosis.—Colony encrusting. Zooecia small, plump, crowded but in linear rows. Front convex, nonporous except for some small areolae (fig. 19 A). Orifice hemispherical above, contracted and with small lyrula below (fig. 18 M); five to seven oral spines (fig. 8, 9 Q). Avicularia small, rounded, oriented at a 60° angle to the plane of the orifice (approximately). Mandible semicircular. Avicularial chamber limited to region immediately around proximal orifice border. Peristome (fig. 12 V) unevenly developed. Ovicell (fig. 10, 12 S) hyperstomial, opening into the peristomie. Ancestrula with about six oral spines.

Measurements.—See page 234.

0.232–0.421 (0.328) L Zooecia
0.145–0.290 (0.228) W Zooecia
0.044–0.087 (0.059) L Avicularia
0.044–0.080 (0.059) W Avicularia
0.148–0.196 (0.170) L Ovicells
0.174–0.215 (0.197) W Ovicells
0.131–0.174 (0.147) Ovicell, front to back diameter
0.065–0.080 (0.071) L Primary orifice, untipped, just as zoids lie on their back
0.087–0.109 (0.100) W Primary orifice
0.172 L and W Ancestrula, 1 reading only.

Zoarium.—At first glance *P. marsupium* was thought to be a *Cellepora* because of its very small crowded zoids and hidden orifices but a closer study of the orifice proved it to be a *Porella*.

Only small encrusting colonies of few zoids and but a few millimeters across were found.

Zoecium.—Zooecia have a quincuncial arrangement near the center of the colony (fig. 9) but may tend to form more orderly linear rows (fig. 10, 12) when the substratum permits. The zooecial front is convex, calcareous, granulated and nonporous except for the occasional small areolae (fig. 19 A). A prominent spoutlike umbo (fig. 9, 10, 12 Z), topped by a rounded avicularium, rises just in front of the orifice. The umbo of specimens from Sta. 240z rock had a prolonged peak in front of the avicularium (fig. 16).

The umbo forms the peristome. The peristome extends around the front and sides of the orifice. At the sides the peristome may develop into an extended flap (fig. 12 V).

Young nonovicelled zoids have five to seven thin long oral spines (fig. 9 Q). In older zoids the lateral peristome grows in height replacing some of the lateral oral spines which have broken off, incorporating their bases. The ovicell begins to form on some zoids before the distal spines are lost.

Avicularium.—The umbo rises at a 60° slant, approximately, from the frontal wall. The oral avicularium is on its distal oral side, likewise at about a 60° slant, away from the orifice.

Only these small median suboral avicularia were found, one per zoid. Though somewhat variable in size the avicularia look alike. Their semicircular mandible points away from the orifice.

The umbo houses the hemispherical or crescentic avicularial chamber (fig. 11, 17 C) whose lateral extremities do not extend to lateral areolae, thus differing from some of the other

Smittinidae. In some zoids two small pores (fig. 18) occur on the inner surface of the frontal wall which forms the avicularial chamber floor. Not enough good specimens were available to check if this is a constant condition.

Orifice.—The deeply buried primary orifice is semicircular distally (almost) and contracted proximally. It has a small, low, median lyrula and slight lateral cardelles or condyles with which the operculum articulates. Busk's *L. marsupium* lacked a lyrula and its operculum was different from that of the USN specimens.

The frontal wall of the next distal zoid does not encroach upon the peristome.

Ovicell.—The bulbous hyperstomial ovicells open into the peristomie (lumen of the peristome) and are not closed by the operculum. Their opening is hidden from view because of the angle at which the ovicell is tipped forward (fig. 10, 12).

The ovicell surface is granulated, generally nonporous. In Station 240 colonies ovicells as well as umbos, tended to develop a small peak frontally.

A Station 226 colony had several ovicells each of which was half-filled by a small red embryo.

Oral spines remain for a short time about the orifice while the ovicell is developing, then break off near the base where there may be a "joint." Two spines remain for some time after the ovicell is well formed, one at each side of the ovicell distal to the peristomial flaps.

Distribution and ecology.—This species was not abundant. The small *P. marsupium* colonies came from the USN Antarctic Stations 104 of the Ross Sea Area and Stations 190, 226, 238, 240 of Marguerite Bay. It grew on various substrates: rhizoids of bryozoans or hydroids (Sta. 190, 226); sponge spicules (Sta. 190); *Notoplites tenuis* (Sta. 104, 238); rocks (Sta. 240); fragments of mollusk shell, algae and *Phylactellipora lyrulata* (Sta. 226).

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